some other factor is responsible can only be revealed by future studies.

Townsendia, for the most part, is confined to rather high altitudes in the Rocky Mountains. From my preliminary survey of the genus it is apparent that certain mountain ranges possess distinctive races or species. A critical correlation of the geographical distribution and morphological variation in the genus should reveal the effects of isolation and the origin of new forms or species.

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SOME PARALLELS BETWEEN DESERT AND ALPINE FLORA IN CALIFORNIA

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At first sight it may seem that a desert flora is the opposite of an alpine flora, just as the climatic conditions seem so different. The alpine flora is usually largely influenced by the long cold winters, whereas the desert flora derives its specific character from the hot summers and lack of water.

A comparison will be made between the flora of the central and southern Sierra Nevada (Yosemite and Sequoia National parks) and the Mohave and Colorado deserts of California. In and around these deserts several mountain ranges reach into the alpine zone so that a continuous range of climatic conditions links the two chosen areas; for comparison, however, the extremes will be discussed: montane and alpine conditions at 2000 meters and higher, the desert conditions below 1000 meters.

The alpine climate is one of a very short growing season of about two months duration (July and August) at altitudes of 3000 meters (Clausen, Keck, and Hiesey, 1940) and a little longer at 2500 meters. Due to the relatively small precipitation, snow cover is in most localities not the limiting factor determining the beginning and end of the growing season. Only towards the end of June do the mean minimal daily temperatures reach values near 0° C.; before that the freezing point is reached every night, which makes growth for most plants impossible. Melting snowbanks indicate how few plants can develop at all temperatures around the freezing point. *Erythronium, Caltha biflora* and some *Carex* species are examples of plants which can grow to a very limited extent under melting snow, which means at 0° C., but most other plants covered by snow (such as *Salix*) do not start to show visible signs of growth until the snow has disappeared. Since in most plants actual growth occurs during night, no appreciable growth is possible until the night temperatures remain above the freezing point. And in the beginning of September the nights become too cold again for growth. Day temperatures during the growing season become quite high (20 to 25° C.). Precipitation is very limited during the growing season, usually not exceeding 40 mm. during the growing period, and is irregularly distributed as thunderstorms. Therefore the plants have to depend on soil moisture, which restricts their distribution. Also it increases the percentage of xerophytic plant types compared with the moister alpine regions of the mountains farther north. Yet the main limitation of growth is due to low temperatures.

In the lower deserts of southern California the rainfall occurs almost exclusively during the winter, when temperatures are fairly low; at sea level freezes occur only seldom, but, at altitudes around 1000 meters, growth during the winter months is suspended due to low temperatures. Then a short growing season (March through May) follows before the soil is too dry for further plant development.

Therefore the desert and alpine climates have in common a very short growing season: in the desert it is limited by cold in the beginning and by moisture in the end, and under alpine conditions it is limited by cold both as far as beginning and end are concerned, dryness also entering in as a factor. During the growing season in both localities a high rate of insolation and extremes in daily range of temperature are common, especially low night temperatures. Considering all this it is not amazing that marked parallels in vegetation occur.

Whereas at least one-half of the California alpine plants belong to genera migrating from the north (*Achillea, Aquilegia, Androsace, Antennaria, Carex,* various conifers, *Draba, Epilobium, Pedicularis, Potentilla, Primula, Ranunculus, Saxifraga, Silene, Tofieldia* and *Viola*), a considerable number developed from typically Western North American genera. In general the latter genera have a much wider distribution over California than those coming from the north. In Table 1 the approximate altitudinal distribution of the circumboreal and Western North American genera is shown. Most of the data are taken from Jepson's Manual (1925) with occasional additions and changes based on personal observations. In general the altitudinal range for most species is higher in the southern Sierra Nevada than indicated by Jepson.

Table 1. Approximate Altitudinal Distribution of Circumboreal and Western North American Genera

Genera with circumboreal distribution	No. of California species total	Main distribution above 2000 m.	Per cent alpine species	Genera with main distribution in Western America	No. of California species total	Main distribution above 2000 m.	Per cent alpine species
Anemone	5	3	60	*Brodiaea*	21	3	12
Antennaria ..	8	8	100	*Calochortus* ...	24	4	17
Arenaria	14	7	50	*Ceanothus*	29	5	17
Arnica	10	7	70	*Collinsia*	17	7	41
Carex	127	58	46	*Delphinium*	16	5	31
Crepis	8	4	50	*Erigeron*	32	15	47
Draba	12	9	75	*Eriogonum*	66	18	27
Epilobium ...	13	10	77	*Eriophyllum* ..	13	4	31
Hieracium ...	7	3	43	*Gilia*	19	6	31
Pedicularis ..	6	5	83	*Mimulus*	39	12	31
Pirola	6	4	67	*Monardella*	19	5	26
Potentilla	44	30	68	*Penstemon*	37	20	54
Salix	22	12	54	*Phacelia*	55	11	20
Saxifraga	10	8	80	*Ribes*	26	10	38
Silene	21	10	48	*Solidago*	8	2	25
Stellaria	8	4	50	*Streptanthus* ..	21	7	33
			64%				30%
Mean	20.1	11.4	57%		27.6	8.4	30%

This table shows what was to be expected: the genera migrating from the north have remained in the cooler regions, and relatively few species have adapted themselves to the lower and warmer regions of California. Many of those occurring at lower altitudes are directly derived from or are identical with forms occurring elsewhere at lower altitudes (*Arenaria, Carex, Crepis, Hieracium, Salix, Silene, Stellaria*). Others occur at lower altitudes only in the cool, moist northwestern part of California.

The endemic genera on the other hand have developed everywhere, and have representatives not only in the mountains, but also in chaparral, deserts and valleys. Therefore the percentage of their occurrence in the mountains is lower. However, another factor enters into the problem, and this is moisture. Most of the northern genera require a fairly high amount of moisture, at least in the soil, during the growing season. The species of these genera which have invaded the lower regions usually occur in moist places, thus having acquired only the ability to grow at higher temperatures without having altered their water requirements.

In contrast with the origin in the north of about 50 per cent of the entire alpine flora, when we consider the annuals alone occurring at an altitude of 2700 meters and higher, 75 per cent of them belong to endemic genera. Only the species belonging to circumboreal genera have a distribution reaching beyond California as far north as Washington and Alaska, as the following list shows. There are more annual species known which reach up into the alpine zone, but most of these belong to the genera listed below (Table 2). Some others, like *Gnaphalium purpureum* and *G. palustre,* have a much lower distribution, and under exceptional conditions are found in the alpine zone.

Table 2. Distribution of Species Considered

Species	Distribution
1. *Collinsia parviflora*	Mount Shasta to Mount San Jacinto
2. *Collinsia Torreyi*	Mount Shasta to southern California
3. *Cryptanthe Torreyana*	Mount Shasta to Sequoia National Park
4. *Eriogonum spergulinum*	Sierra Nevada
5. *Gayophytum humile*	Washington to southern California
6. *Gayophytum ramosissimum*	Mount Shasta to southern California
7. *Gilia leptalea*	Northern California to Sequoia National Park
8. *Linanthus ciliatus* var. *neglectus*	Southern Sierra Nevada
9. *Linanthus Harknessii*	Idaho to Yosemite National Park
10. *Mimulus leptaleus*	Mount Lassen to Sequoia National Park
11. *Mimulus montioides*	Northwestern Nevada to Sequoia National Park
12. *Mimulus rubellus*	British Columbia to southern California
13. *Nemophila spatulata*	Western Nevada to southern California
14. *Streptanthus tortuosus*	Mount Shasta to Sequoia National Park
15. *Draba stenoloba*	Alaska to Sequoia National Park
16. *Galium bifolium*	Washington to Yosemite National Park
17. *Juncus triformis*	Washington to southern California
18. *Polygonum Kelloggii*	British Columbia to southern California
19. *Polygonum minimum*	Alaska to Yosemite National Park

In the Swiss Alps six to thirteen annual plants occur above 2500 meters. Since 2500 meters in the Alps corresponds climatically with 3500 meters in the Sierra Nevada,[1] where almost no annuals are found at 3500 meters (only occasionally some *Mimulus* species, Sharsmith communication), the population of alpine annuals in the Sierra Nevada is relatively poor. This is obviously connected with the limited and unreliable precipitation during summer, which does not favor the development of annuals. It is significant, however, that the annuals occurring are predominantly representatives of endemic Western American species. In the Olympic Mountains of Washington only one single annual (*Polygonum minimum*) is found above timberline. Table 3 gives a comparison of the number of annuals found at corresponding altitudes in Europe (taken from Raunkiaer, 1908) and the Sierra Nevada.

[1] Timberline in the Alps is 2200 meters at the highest, but in general it is around 2000 meters, whereas timberline in the southern Sierra Nevada lies as high as 3100–3300 meters.

TABLE 3. COMPARISON OF THE NUMBER OF ANNUALS FOUND AT DIFFERENT ALTITUDES IN EUROPE AND THE SIERRA NEVADA

Altitude in respect to timberline	Poschiavo	Tatra	Western Alps	Aosta Valley	Sierra Nevada
+ 700 m. – higher	1		3	5	
+ 350 m. – + 700 m.	8	1	13	6	
timberline – + 350 m.	22	9			
– 350m. – timberline	30	28			19
– 700 m. – 350 m.	39				

From these considerations we can draw an interesting conclusion. The climatic response of a genus or even a family is a physiological character which is extremely tenacious, and can hardly be changed by evolution. Temperature tolerance, drought resistance, water requirements all seem to be physiological characters, which are as constant and as unalterable as generic or family characters, and are not of the type which are usually encountered in genetic variability. Thus most alpine annuals in the southern Sierra Nevada are really desert annuals with a higher altitudinal distribution. The following list shows how many of the alpine annuals of endemic genera have close relatives in desert regions (Table 4). *Nemophila* is a genus of moist places, but closely related genera (*Ellisia, Phacelia*) have many desert annual species. *Gayophytum* is an exclusively montane genus, but with many desert species in related genera (*Oenothera, Gaura*).

Apart from the relations between desert and alpine therophytes, there are many parallels between perennial plants, shrubs and trees in desert and alpine habitat. These are all basically conditioned by the short growing season with limited moisture, high insolation and large temperature fluctuations. A partial list of plants occurring in both habitats follows:

A. Geophytes (bulbous plants) : *Calochortus, Brodiaea.*

B. Phanerophytes (trees). At the extreme range it is in both conditions conifers which dominate. *Pinus monophylla* and *Juniperus* are the first trees to appear at the upper range of the desert steppe, where rainfall becomes slightly greater. *Pinus albicaulis, P. flexilis, Juniperus occidentalis, Tsuga Mertensiana* and some other conifers are the last trees found above 3000 meters.

The Joshua tree (*Yucca brevifolia*) has no counterpart in the Sierra Nevada and a large number of moisture-loving shrubs of the alpine habitat have no relatives or analogs in the desert. But in any case the number of deciduous trees and shrubs is small in both habitats.

C. Hemicryptophytes and Chamaephytes. In both habitats we commonly encounter the rosette habit, which has developed into the cushion habit under alpine conditions, but is common as

Table 4. Alpine Annuals of Endemic Genera Having Close Relatives in Desert Regions

Alpine species	Altitudinal range	Desert species	Altitudinal range
Collinsia parviflora	1500–2500 meters	*Collinsia Davidsonii*	1000 meters
Collinsia Torreyi	1000–3000 "		
Cryptantha glomeriflora	2000–3000 "	*Cryptantha angustifolia*	0–1500 "
Erigonum spergulinum	2000–3000 "	*Eriogonum gracillimum*	0–1500 "
		Eriogonum inflatum	0–1500 "
Gilia capillaris	2000–2500 "	*Gilia latifolia*	0–1500 "
Gilia leptalea	500–3000 "	*Gilia filiformis*	500–1500 "
		Gilia ochroleuca	500–1500 "
Linanthus ciliatus	2000–3000 "	*Linanthus maculatus*	0–1000 "
Linanthus oblanceolatus	2500–3000 "	*Linanthus Parryae*	500–2000 "
Linanthus Harknessii	1500–3000 "	*Linanthus Bigelovii*	500–1500 "
Mimulus leptaleus	2000–2500 "	*Mimulus Bigelovii*	0–2000 "
Mimulus montioides	2000–3500 "	*Mimulus mohavensis*	500–1000 "
Mimulus rubellus	2000–3000 "		
Streptanthus tortuosus	2000–3000 "	*Streptanthus inflatus*	500–1000 "

regular rosettes in the desert. Probably both the cushion and rosette habit have the same basic evolutionary significance: 1) low night temperatures counteract stem elongation without interfering too much with organ initiation, 2) during the short growing season no material is squandered on synthesis of stem material, 3) it gives snow and grazing protection.

D. Typical of both alpine meadows and deserts is the mass flowering, in deserts in April and in alpine meadows towards the end of July. This is probably also associated with the short growing season, which forces all plants to flower at approximately the same time, to have a chance to ripen their seed before cold or drought cuts short further development.

E. Table 5 lists closely related perennial species which occur in deserts and under alpine conditions. In this list occur a few plants which are represented by annual species in the desert (e.g. *Calyptridium monandrum*) but by perennial species in the alpine region (*C. umbellatum*).

If we analyze Table 5 together with the list of alpine annuals (Table 2) the following general distribution of these genera over the world is found:

Cosmopolitan (occurring on more than two continents)	13
North and South America	8
Northern Hemisphere	4
General North America	2
Western North America only	13

This shows clearly how important the evolutionary pressure favors the endemic genera, in developing both desert and mountain forms. Actually the percentage of genera with strong endemism is much greater, since many plants (e.g. *Lupinus*, *Astragalus*) listed under cosmopolitan or other headings, have a strong endemic development in Western North America.

In general it seems more common for a desert plant to develop an alpine relative than for alpine plants to develop forms which

TABLE 5. GENERA WITH REPRESENTATIVES BOTH IN DESERTS AND MOUNTAINS, ARRANGED ACCORDING TO FAMILIES

Family	Alpine species	Desert species
Filices	*Pellaea Bridgesii*	*P. ornithopus*
	Cheilanthes gracillima	*C. Covillei*
Gymnospermae	*Pinus contorta*	*P. monophylla*
	Juniperus occidentalis	*J. californica*
Gramineae	*Muhlenbergia andina*	*M. Porteri*
	Sporobolus confusus	*S. airoides*
	Oryzopsis Kingii	*O. hymenoides*
	Stipa minor	*S. speciosa*
Liliaceae	*Brodiaea gracilis*	*B. capitata*
	Calochortus Leichtlinii	*C. Kennedyi*
Polygonaceae	*Eriogonum incanum*	*E. Heermannii*
Portulacaceae	*Calyptridium umbellatum*	*C. monandrum*
Cruciferae	*Streptanthus tortuosus*	*S. inflatus*
Leguminosae	*Lupinus superbus*	*L. rubens*
	Lotus oblongifolius	*L. scoparius*
	Astragalus Hookerianus	*A. tricarinatus*
Euphorbiaceae	*Euphorbia Palmeri*	*E. polycarpa*
Loasaceae	*Mentzelia congesta*	*M. tricuspis*
Onagraceae	*Oenothera subacaulis*	*O. scapoidea*
Umbelliferae	*Cymopterus terebinthinus*	*C. panamintensis*
Gentianaceae	*Swertia albomarginata*	*S. perennis*
Hydrophyllaceae	*Phacelia heterophylla*	*P. calthifolia*
	Nama Rothrockii	*N. demissum*
Boraginaceae	*Cryptantha glomeriflora*	*C. racemosa*
Scrophulariaceae	*Penstemon Menziesii*	*P. ambiguus*
	Castilleia minor	*C. angustifolia*
Compositae	*Haplopappus eximius*	*H. gracilis*
	Aster integrifolius	*A. Orcuttii*
	Erigeron compositus	*E. Parishii*
	Hemizonia Wheeleri	*H. Wrightii*
	Eriophyllum lanatum	*E. Wallacei*
	Chaenactis nevadensis	*C. Fremontii*
	Artemisia Rothrockii	*A. spinescens*

survive in the desert. Since in both cases the plants are adapted to short growing periods, violent temperature fluctuations and low night temperatures, we might conclude either that genera in strong evolutionary development (with many endemic species) have greater inherent adaptability, or that adaptation to frost resistance is more common than adaptation to drought resistance. Yet the Cactaceae have no alpine representatives; neither have *Agave, Fouquieria,* Zygophyllaceae nor other typical desert plants.

It might seem that the plants used by the Carnegie Laboratory group at Stanford University disprove the conclusions reached above. A number of plants with a very wide altitudinal distribution has been investigated (Clausen, Keck and Hiesey, 1940), some of them belonging to boreal genera (*Achillea lanulosa, Viola purpurea, Aster adscendens, Potentilla glandulosa, P. gracilis*). These plants, however, are exceptions to the rule and were deliberately selected among the whole vegetation of California because of their exceptionally wide altitudinal and latitudinal distribution. With such exceptions we can say that the great majority of species has a fairly limited range of distribution. This is surprising in view of the fact that the same temperatures occurring in July and August at 3000 meters altitude, occur in May and October at 1500 meters and in February and November at sea level. Therefore a summer plant at high altitudes might grow as a spring or autumn plant at lower altitudes and be subjected to exactly the same temperatures. There are a few plants which behave in this way, like *Erysimum asperum,* which flowers in February at sea level and in July at timberline, but the majority of plants do not shift their growing season, thus enabling them to occur at different altitudes. This is due to other climatic factors such as photoperiod, chilling requirement, and seasonal succession of temperatures. And this brings us back to the original thesis, that the physiological responses to climatic factors are only very little changed in the course of evolution.

Summary

The close relationships of many desert and alpine plants in California is pointed out. This resemblance is greatest for the alpine therophytes (annuals) of which 75 per cent have close relatives in the desert. This is due to several reasons:

1) Climatically the desert and alpine habitats are alike during the actual growing season.

2) Whereas part of the alpine flora is of circumboreal origin, at least one-half belongs to genera endemic in Western North America, which are exactly those which have also developed representatives in the desert.

When comparing the altitudinal distribution among the alpine plants of the circumboreal genera with those endemic in Western North America, it was concluded that in general the climatic re-

sponse of a genus or a family is only very little affected by evolution. This climatic response is due to physiological characters, such as temperature requirement, frost and drought resistance, and water requirement.

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SOME ADDITIONAL NOTES ON POLEMONIACEAE

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The preparation of the manuscript for the treatment of Polemoniaceae in Abrams, Illustrated Flora of the Pacific States, demands that certain points not suitable to develop in that publication be made clear elsewhere. These are the publications of certain new species and subspecies and the discussions of reasons for some of the decisions made where problems seem controversial. Most of the present notes concern the genus *Linanthus.* A new species of *Collomia* is also included.

Linanthus androsaceous Benth.

The treatment afforded this species calls for the aggregation of several entities traditionally regarded as distinct, as subspecies under *L. androsaceous* Benth. This move appears imperative because there seems to be no way to differentiate these subspecies clearly from one another because they show intergradation of a type that suggests wholesale introgression. What appears to have happened is that there developed under the sanction of insular isolation of late Tertiary time a large number of distinct types which, when the continent assumed its present form, were permitted to mingle, apparently without effective genetic barriers between them. The result is the present morphological confusion in the coast ranges of California and Oregon. Where colonies have persisted under conditions of isolation they have retained a certain local uniformity. One such colony occurs in the Sierra Nevada foothills and necessitates formal description as a new subspecies.